JOURNAL

OF THE

WASHINGTON ACADEMY OF SCIENCES

Vol. 31 April 15, 1941 No. 4

ECOLOGY.—*Adaptive coloration in a single faunal association.*[1]

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The meaning and methods of adaptive coloration are stated so fully in Cott's recent book (1940) that a general survey of the subject may not be needed again for some years. Rather his work, with its large bibliography, should stimulate special studies and detailed applications of principles. One such problem that has not yet received adequate treatment is the effect of adaptive coloration on the total population of a single ecological association.

An association particularly favorable to such study is the rain forest of Barro Colorado Island in the Canal Zone, now receiving maintenance as a biological reservation from the United States Government. The writer collected there in the summer of 1939.

Barro Colorado Island, in Gatun Lake, is about 6 square miles in area, almost entirely covered by climax rain forest. Over 700 species of trees occur there, the dominant crowns of a few, such as *Bombacopsis felderi*, exceeding 200 feet in height. Most species are broad-leaved hardwoods. A litter of fallen leaves covers the ground nearly everywhere, averaging 1 to 4 inches in depth, but decomposition of this litter is so rapid that the red lateritic clay soil begins directly under it with scarcely any or humus layer. The undergrowth varies in density but in most places is not thick enough to interfere with walking. Although there is little standing water on the island, numerous small streams run down to the lake, their beds being generally of blackened pebbles and boulders.

Thus the niches available for the rain-forest fauna (apart from burrowing, subterranean or aquatic forms) are the following:

1. Trees: Foliage, limbs, trunks, crevices.
2. Epiphytic vegetation, including lianas, bromeliads, ferns, mosses, etc.
3. Undergrowth: Foliage, stems.
4. Ground surface, on or under leaf litter.
5. Ravines, stream beds, banks, bare trails, beaches (a relatively small area).

[1] Received February 15, 1941.

ECOLOGICAL RELATIONSHIPS OF THE TYPES OF COLOR ADAPTATION

I. Color adaptations among rain-forest animals are numerous and varied. Cott (1940) groups them as concealment, advertisement, and disguise. There is a strong correlation between adaptive appearance and the diurnal-nocturnal rhythm. Species that are quiet by day and active by night almost invariably show either concealment or disguise in some form, provided they spend the day in a place exposed to the view of animals that hunt by sight. Many species that are active by day, but that spend a part of that time at rest in such places, show the same thing when they are at rest. Species that mimic others exhibit this feature by day, although in some cases they are nocturnal as well. Warning, display, allure, or directive markings function by day, the species very frequently being active both day and night. Adaptive coloration apparently does not occur among animals that burrow or hide out of the ordinary field of vision. It is lacking, for instance, in certain moths (Pyralidae, Geometridae) and butterflies (Hesperiidae, Erycinidae) that alight regularly on the under sides of leaves, showing themselves only while in rapid flight. Thus adaptive coloration is limited to the species that might be visible by day, and, if seen, accessible, whether as prey or as predators.

II. Relationship between adaptive coloration and niches in the rain-forest association:

A. *Obliterative* or *procryptic* coloration occurs in species that rest or pause against a relatively homogeneous background, that is, one in which separate objects mean little or do not show. This must be interpreted in each case from the standpoint of a casual observer. The animal comes within the field of vision but is so colored that it is not noticed as an object. Backgrounds available for obliteratively colored species on Barro Colorado are these:

(1) Surfaces of green leaves. For obliterative effect any surface must be larger than the animals on it, i.e., sufficient to serve as a background. The eggs, larvae, and chrysalids of many Lepidoptera, the adults of some (Geometridae especially), many Coleoptera, Hemiptera, Homoptera, and Orthoptera, some spiders and some tree frogs are cryptically colored on green leaves.

(2) Foliage en masse. Certain larger animals show an obliterative green against the background of massed foliage, which from a distance can be regarded as homogeneous. Such are the green tree-snakes, lizards like *Polychrus gutturosus* and *Iguana iguana*, and many, if not all, of the green birds.

(3) Tree trunks, root buttresses, fallen logs. Procryptic animals here include Lepidoptera (Noctuidae, Notodontidae, Geometridae, Sphingidae, some nymphalid and brassolid butterflies), many caterpillars, Coleoptera such as cerambycids, elaterids, and some prionids, certain spiders, tree frogs, and geckos.

(4) Leaf litter, probably 99 per cent of the ground cover in the forest. Animals deceptively colored like this background include Lepidoptera (Noctuidae, Notodontidae, Geometridae, Satyridae, Nymphalidae, and others), some Orthoptera and spiders, many frogs, toads, lizards, and snakes, ground birds such as tinamous and (by day) nighthawks. Many of the Lepidoptera show a partial leaf-vein pattern on their wings, but the shape of the wings is usually not leaflike, since obliteration rather than object-imitation is the result achieved. Satyrid butterflies of the genus *Pierella* are common examples of this. While the leaf litter is relatively homogeneous as a background, enough contrast of light, shade, and sharp edges occurs to cause disruptive patterns frequently to accompany obliterative coloring in the species that occupy this niche.

(5) Bare ground, as mud beside streams, open trails, banks, etc. A dark purple-brown *Cicindela* is common and procryptically colored on the trails, so that only careful watching will detect it before it flies. The tendency of many species of tiger beetles to show the color of their background is familiar. Dice and Blossom (1937) recently pointed out that the same is true of local races of *Peromyscus* living in open, arid country, but is less likely to occur in covered areas.

B. *Disruptive pattern* is common in connection with obliterative background resemblance. Its effect is to add a seeming discontinuity to the procryptic effect already achieved. An excellent example, one among many in Lepidoptera, is the large, brown satyrid *Antirrhaea miltiades*, in which a white blotch and streak on the hind wings destroy any probable recognition of the butterfly as a separate object when it alights on dead leaves. The remainder of the pattern is dead-leaf brown. Most cases of deceptive rupture of pattern will probably be found to work when the rest of the pattern is obliterative and the background moderately heterogeneous. Accordingly the leaf-litter fauna should be, and is, particularly rich in this kind of adaptive coloration. Species on pebbly ground and on rough tree trunks often show it as well.

C. *Object resemblance.* Cott uses the term "disguise" to cover this and the usual mimicry between species. "Object resemblance" expresses somewhat more exactly the meaning of the present category.

This type of deception is found in niches occupied largely by discrete objects, such as leaves, twigs, or thorns. Species that resemble these objects do so by adaptation not only of color but of form. The disguise is most effective while the animal is motionless, except when the objects in question happen to move, in which case the animal may do so. Many of the amazingly twiglike Phasmidae (Orthoptera) sway rhythmically from side to side like twigs in a breeze. Certain Mantidae have also become twiglike. *Dinopis*, a spider, fits its legs together in line with the body and hangs motionless like a piece of dead twig on an inconspicuous thread. Among the twig-imitators should also go the spider that prepares a line of frass with a half-inch gap, into which it then fits and so completes the artificial twig. Twiglike geometrid larvae are common, as are the thornlike membracids. It is a rule that these types occur in places where the particular thorns or twigs they resemble also prevail.

Examples of leaf-imitation involving the color, pattern, and form of leaves are: Leaf-mantids (some resembling living, others dead leaves), leaf-butterflies, and a few large moths, like *Ophideres*, which hangs in a most convincing manner like a dead leaf from the stem of a low bush.

D. *Transparency.* It is, of course, impossible for a flying insect to achieve complete transparency, although many aquatic organisms, including prawns in Gatun Lake, have nearly or quite done so. Yet a filmy translucence affecting the larger part of the insect has a highly deceptive function. Sometimes it is combined with a contrasting pattern, as in some of the largest forest damselflies (Zygoptera, Coenagrionidae), where at the tip of each wing is a yellow, white, or blue spot, and the insect as a whole is difficult to see in flight because almost nothing shows but these separated, vibrating spots. Transparency has developed among butterflies in more than one shade-living group independently, the most important being Ithomiidae. *Ithomia, Leucothyris*, and some other genera are partly transparent and deceptive while flying in the gloom of the forest. They do not occur in strong light. *Cithaerias menander* is a transparent satyrid, also occurring in deep shade. Across its wings are faint vestiges of the leaf-vein lines that are present in some allied brown satyrids with an obliterative dead-leaf pattern. This suggests that *Cithaerias* has changed a former obliterative appearance for transparency, equally deceptive and functioning in flight as well as at rest.

E. *Mimicry* between unrelated species is a type of deception that *reduces the total number of apparent species* in a given ecological association. This is accomplished by duplication of color, pattern, form, and behavior, at least outwardly. A mimetic group of unrelated species, consisting of two to six or more species, thus appears to be one by sharing a particular configuration.

The term "configuration" is used here to imply a connection with the Gestalt theory of learning. Each mimetic group, appearing to be a species, is a configuration or "Gestalt" to the predator, and a response of avoidance or acceptance is learned on the basis of experimental or haphazard encounters between the predator and its prey. A reduction of the number of Gestalten to be recognized can only simplify the learning process, by reducing the number of encounters needed to fix a given Gestalt in the predator's memory. Mimicry accomplishes this reduction. The learned response to a mimetic group appears in every case to be avoidance, since this kind of Gestalt happens to provide a disagreeable experience in a large proportion of possible encounters.

Mimicry observed in Panama shows, as a whole, no definite correlation with ecological niches, except that, like other adaptive coloration, it functions by day within the field of vision of species that hunt by sight. Mimetic groups seen were the following:

(1) Mutillid wasp, female, mimicked by cicindelid beetle.

(2) Winged wasps (probably a complex including models for several different mimetic groups), mimicked by certain Diptera, staphylinid beetles, euchromiid moths.

(3) Bees, mimicked by numerous Diptera.

(4) Ants, mimicked by spiders (especially attids), by cerambycid beetles, and by a mantid. Here again more than one mimetic group occurs, for the ants mimicked by the mantid are ponerids, while those mimicked by the spiders and beetles are various formicids.

(5) Lycid beetles, mimicked by euchromiid moths (*Dycladia*, *Correbia*, *Correbidia*) and by arctiids (*Lycomorphodes*, Forbes, 1939). Many other insects have been reported as lycid mimics in Asia and Africa (Carpenter, 1920).

(6) A lampyrid beetle, mimicked by an arctiid moth, *Diarhabdosia*.

(7) Danaid butterflies, mimicked by ithomiids, papilionids, and female pericopid moths.

(8) Heliconid butterflies, mimicked by ithomiids and pierids.

(9) *Papilio* (some of the *Aristolochia*-feeding species), mimicked by certain pericopid moths (Forbes, 1939).

F. *Directive* (misleading) markings and behavior. In this category I include the cases in which a part of the animal looks and acts like something it is not, while the remainder is free from any deceptive effect, and may, indeed, be highly conspicuous. This comes under "advertisement" in Cott's (1940) work. Many of the hair-streak butterflies (Theclinae) have on the under side of the wings a showy pattern of lines and stripes, visible when they alight with wings upright. At the posterior end of the hind wings is a red or orange spot, beyond which one or two hairlike tails project. The butterfly, when at rest, constantly moves the hind wings up and down against each other, imparting a writhing motion to the spot and active wriggling to the tails. Whether this is a "false head" with "false antennae" to lure possible attackers away from the "vital" to some "nonvital" part of the body is a question on which agreement may be difficult; it is a fact that one is temporarily deceived as to the actual head of the insect, and that insectivorous birds and lizards usually respond to moving rather than motionless objects.

G. *Warning* and *display*. Deception is a minor factor in this kind of advertisement, except when the species are already deceptive through mimicry, as with the color-display and fake stinging motions of the wasplike staphylinid beetles. A more typical case of simple "warning" is the bright green and shiny black pattern of the frog *Dendrobates auratus*. This species is common in the forest of Barro Colorado, active by day and night, and a highly conspicuous animal for its size. Its poisonous skin secretion is quickly associated with the striking colors.

CONCLUSIONS

1. The kinds of adaptive coloration occurring in the rain-forest fauna are correlated with particular niches in that association. Obliterative color and pattern occur where the background is relatively homogeneous. Obliterative-ruptive patterns are correlated with a more heterogeneous background, yet one in which separate objects mean little. Object-resemblance is common in an environment composed of discrete details (leaves, twigs, thorns). Transparency occurs in shade-dwelling, large-winged insects. Mimicry reduces the apparent number of species to be recognized. Directive markings, warning, display, and the lack of adaptive coloration show no specific environmental correlation, except that species which burrow or hide out of the ordinary field of vision are unlikely to be adaptively colored in any way.

2. The total population, both of species and of individuals, occupying this faunal association appears to be much greater than would be possible in the absence of adaptive coloration, because (a) species

with obliterative, disruptive, object-imitative, or mimetic adaptations are less frequently noticed, or, if noticed, are avoided; (b) those with misleading markings or deceptive transparency may be noticed but remain relatively inaccessible; (c) those with warning coloration associated with disagreeable traits are usually avoided. To express this in figures would mean little, however, since (a) enormous groups rather than a few species are involved, (b) relatively few species-determinations of rain-forest insects from any one locality are available, and (c) the ratio between adaptively and nonadaptively colored species must be, in the nature of the case, inconstant.

Since the recent literature, very adequately cited by Cott (1940), contains evidence on nocturnal behavior, on color vision in insects and other animals, and on the selective value of various kinds of adaptive coloration, this material is omitted from the present paper, although much that is pertinent might be taken from it.

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ZOOLOGY.—*The gender of scientific names in zoology.*[1] Richard E. Blackwelder, U. S. National Museum.

The scientific names of animals, according to the International Rules of Zoological Nomenclature, must be words that are either Latin or Latinized, or that are considered and treated as such in case they are not of classic origin. Both generic and specific names are to be formed according to the principles of Latin grammar and usually have Latin endings. Specific names must bear the proper modifying relation to the generic name and may have a variable ending for this purpose. For example, adjectives must agree in gender with the generic name, substantives in apposition must be in the nominative case, and possessive substantives must be in the genitive case.

Our Zoological Code specifies these principles and some others but

[1] Published with the permission of the Secretary of the Smithsonian Institution. Received November 25, 1940.

A preliminary sheet showing the two tables included in this paper was distributed at the Taxonomists' Conference on Nomenclature at the Philadelphia meetings of the American Association for the Advancement of Science on December 29, 1940. Discussion at that meeting brought out the necessity for changing Table 1. Copies of the sheet should therefore be destroyed or changed to agree with the revised version herein presented.